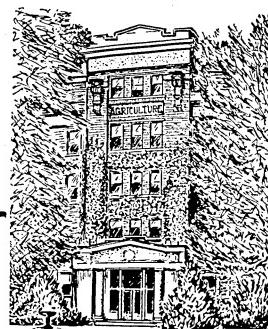


Flight Patterns of Bark and Timber Beetles

Associated with
Coniferous Forests of
Western Oregon

Agricultural Experiment Station
Oregon State University
Corvallis, Oregon



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AUTHORS: G. E. Daterman, formerly a research assistant at Oregon State University, is now with the United States Forest Service Forestry Sciences Laboratory, Corvallis. Dr. J. A. Rudinsky and Dr. W. P. Nagel are forest entomologists, Department of Entomology, Oregon State University. This bulletin is based on a thesis submitted by Mr. Daterman in partial fulfillment of the requirements for a Master of Science degree at OSU.

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Flight Patterns of Bark and Timber Beetles Associated with Coniferous Forests of Western Oregon

G. E. DATERMAN, J. A. RUDINSKY, and W. P. NAGEL

Introduction

Bark and timber beetles of the family Scolytidae are among the most destructive insects of the coniferous forests of the Pacific Northwest, particularly in the coastal subregion where Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, is the principal timber species. Among the bark beetles, the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, killed over three billion board feet of Douglas-fir during the 1951-1954 epidemic; most of the damage occurred in Oregon. The silver fir beetle, *Pseudohylesinus grandis* Swaine, and an associated species, *P. granulatus* (LeConte), were responsible for killing a half billion board feet of silver fir, *Abies amabilis* (Dougl.) Forbes, in northwestern Washington between 1948 and 1955. Among the timber or ambrosia beetles, *Trypodendron lineatum* (Olivier) and *Gnathotrichus* species are the most destructive in this region. Infestations of felled timber by these scolytids cause substantial reductions in market value of wood products. McMullan (1956) reported that, in Canada, ambrosia-beetle damage can cause degrades resulting in 36% monetary loss on plywood veneer and from 2 to 64% on otherwise high-grade lumber pieces. Johnson (1958) stated that similar losses could be expected under American lumber grading rules. In addition, various countries such as Australia, New Zealand, and South Africa enforce embargoes on lumber showing signs of ambrosia-beetle infestation.

The activities of several other scolytids, considered of little economic importance, are of potential interest because of their association with more destructive bark beetles. Such species may be of particular interest as interspecific competitors for available host material, or their dispersal activities may be of significance to related studies of the various bark-beetle predators and parasites.

In order to carry out effective control operations on any of these beetles by sanitation, application of chemicals, or other methods, it is essential to understand how beetle emergence and flight to new host material is influenced by environmental forces. Most bark and timber

beetles spend the majority of their lives within the bark or wood tissues of the host tree, emerging for only brief periods to infest a new host. Since survival of the population depends on the location of new hosts, the importance of this brief dispersal period is readily apparent. Most studies have been concerned with observations of seasonal flight activity and the general biology of the more destructive species. Gara and Vité (1962), however, studying flights of bark beetles in California pine forests, included observations on diurnal as well as seasonal flight patterns. Rudinsky (1963), reporting on the flight and host selection activity of the Douglas-fir beetle, and Rudinsky and Daterman (1964), reporting on the dispersal of *Trypodendron lineatum* and *Gnathotrichus* species, also considered the diurnal aspects of flight. The numerous physical factors that may influence insect flight are comprehensively reviewed by Uvarov (1931) and Andrewartha and Birch (1954).

This bulletin summarizes the diurnal and seasonal flight patterns of scolytid beetles as influenced by various environmental factors, particularly temperature, light intensity, and wind velocity. Brief life histories (as far as known), geographic distribution, and economic importance of each species are given. During these studies, from 1962-1964, 25 beetle species were encountered in the experimental areas, and 10 were present in adequate numbers to allow fuller evaluation: *Pseudohylesinus nebulosus* (LeConte), *P. grandis* Swaine, *Trypodendron lineatum* (Olivier), *Hylastes nigrinus* (Mannerheim), *H. ruber* Swaine, *Gnathotrichus retusus* (LeConte), *G. sulcatus* (LeConte), *Dendroctonus pseudotsugae* Hopkins, *Dryocoetes autographus* (Ratzeburg), and *Scolytus unispinosus* LeConte. The Douglas-fir beetle has been studied intensively in separate projects, and only certain data have been included here for comparison of emergence or flight patterns.

Materials and Methods

The study was conducted on the eastern slope of Marys Peak in the Siuslaw National Forest during 1962, 1963, and 1964, in a 180- to 200-year-old Douglas-fir forest, at an elevation of 1,000 feet. A small percentage of associated conifers is also present in this forest, namely grand fir, western hemlock, and western red cedar. Annual storms and logging operations normally provide a limited amount of fresh host material for the bark and timber beetles. On October 12, 1962, however, winds of hurricane force felled 36 million board feet of Douglas-fir on the Marys Peak watershed, providing 1963 flights of scolytids with an unusually abundant host supply.

Emergence

To compare the time of beetle emergence with the beginning and duration of the spring flights, Douglas-fir logs infested during the previous season were placed in large cages in a clearcut area and also within the stand. Log sections varying from 6 inches to 26 inches in diameter were used. It was felt that this variation in size would provide a good representation of the species infesting the different portions of the stem. Not all species were expected to emerge from this material since several are known to emerge late in the summer and overwinter in the litter, in bark crevices, feeding galleries, and so forth (Kinghorn and Chapman, 1959; Thomas and Wright, 1961). The two sites were used in order to compare the emergence of species from shaded, forested areas and from exposed, clearcut areas. This was considered especially important for this region, where clearcutting is commonly practiced. It was significant that, following bark-beetle flights in 1963, logging operations for salvage of windthrow and felling of storm weakened timber exposed much of the 1963 infested material to clearcut conditions.

Some species are known to re-emerge after establishing a spring brood and to infest additional logs and form a second brood. To relate re-emergence with flight, it was necessary to cage material infested during the initial flights of the insects. During the month of June, after the major flight of most of the species had occurred, log sections known to have been infested earlier in the season were caged in a shaded area of the forest.

At each emergence site, hygrothermographs were permanently housed in small shelters for a continuous seasonal record of temperature and humidity. Mercury thermometers placed inside the cages and inserted beneath the bark of infested logs provided a comparison of air and inner-bark temperatures. As long as emergence activity continued, at least one daily collection was made. On several days of optimum conditions, hourly collections were made to obtain a comparison of emergence activity with flight and the prevailing physical factors.

Sampling nets

Beetles in flight were sampled by rotary nets developed by Gara and Vité (1962). Made of nylon mesh (15 inches in diameter, 28 inches deep), the nets rotated in a horizontal plane 6 feet above the ground on a 58-inch arm (Figure 1). Portable gasoline-engine generators provided power for 0.25 horsepower electric motors which rotated the nets at the rate of 60 r.p.m. Six nets were arranged in a semi-circular pattern, 110 to 140 feet apart; four of them were sta-



Figure 1. Sampling net attached to a six-foot ladder.

tioned under a partially closed forest canopy and two in a stand with a closed canopy. Collections were made hourly, and sampling was terminated in the evening with the cessation of beetle flight. During the early part of the season and through the peak of flight activity, the nets were in operation each day of favorable weather. Beginning in late June, when bark beetle flights decreased sharply, net samples were taken every sixth to eighth day. These intervals proved sufficient for obtaining the seasonal pattern of flight.

In addition to the mercury thermometers placed at the various net positions, hygrothermographs were stationed in the clearcut area and within the stand. Portable wind meters were used to measure air movement. Observations were made and recorded when gross changes in light intensity occurred, such as those caused by sudden overcasts or time of apparent sunset. In May 1964, an illuminometer used with a recording potentiometer provided an accurate measurement of light intensity during a critical period of the flight season. The illuminometer was situated at a height of six feet in an unshaded position.

Effect of attractants

Although it was not within the scope of this study to investigate the response of beetles to attractants, this factor is intrinsically as-

sociated with flight and thus could not be ignored. Net 1 was flanked by split sections of a 180-year-old Douglas-fir, windthrown on October 12, 1962. The sections were arranged seven yards from the net to the north and south. At the beginning of the season, these logs were observed closely for the first infestations in order to make a comparison with the number of scolytids trapped in the nearby net. Such observations were expected to provide an indication of the host attraction *per se* compared to the attraction (if any) produced by attacking species of bark beetle. In addition, the butt portion of a large, old-growth (360-year-old) Douglas-fir, windthrown in October 1962, was lying adjacent to Nets 2 and 3, and 10 and 5 yards away, respectively. This material was also observed for bark-beetle attacks and correlated with the nearby net samples. Since this log varied considerably in bark thickness and possibly physiological condition, it was expected that it might be invaded by different species than the log sections adjacent to Net 1.

Flight Patterns

Definite patterns of seasonal and daily flight activity occurred for each of the species studied. Temperature was generally the most important factor governing activity, although light intensity was of primary importance for certain species. The period of greatest seasonal activity for the majority of species occurred during the first few weeks of warm, clear weather in early spring (Figure 2). The diurnal pattern of flight for many species was similar to that of the Douglas-fir beetle, whose flight activity increases with greater light intensity and rising temperatures within the optimal limits. No scolytids were caught during the nocturnal period, but certain species exhibited definite crepuscular patterns of flight.

Effects of temperature

Some of the more obvious effects of temperature as they commonly influenced the activity of the family Scolytidae as a whole are presented below. More specific findings concerning the effects of physical factors and biotic influences are discussed in relation to the individual species.

Emergence on exposed and shaded sites. As expected, there was a wide difference in the time of emergence between the exposed and the shaded plots. The difference in time for all species was similar to that illustrated in Figure 3 for the Douglas-fir beetle. The earlier emergence in the clearcut area was obviously due to higher prevailing temperatures. In 1963, emergence in the exposed cage began March 19 and 20, whereas activity at the shaded

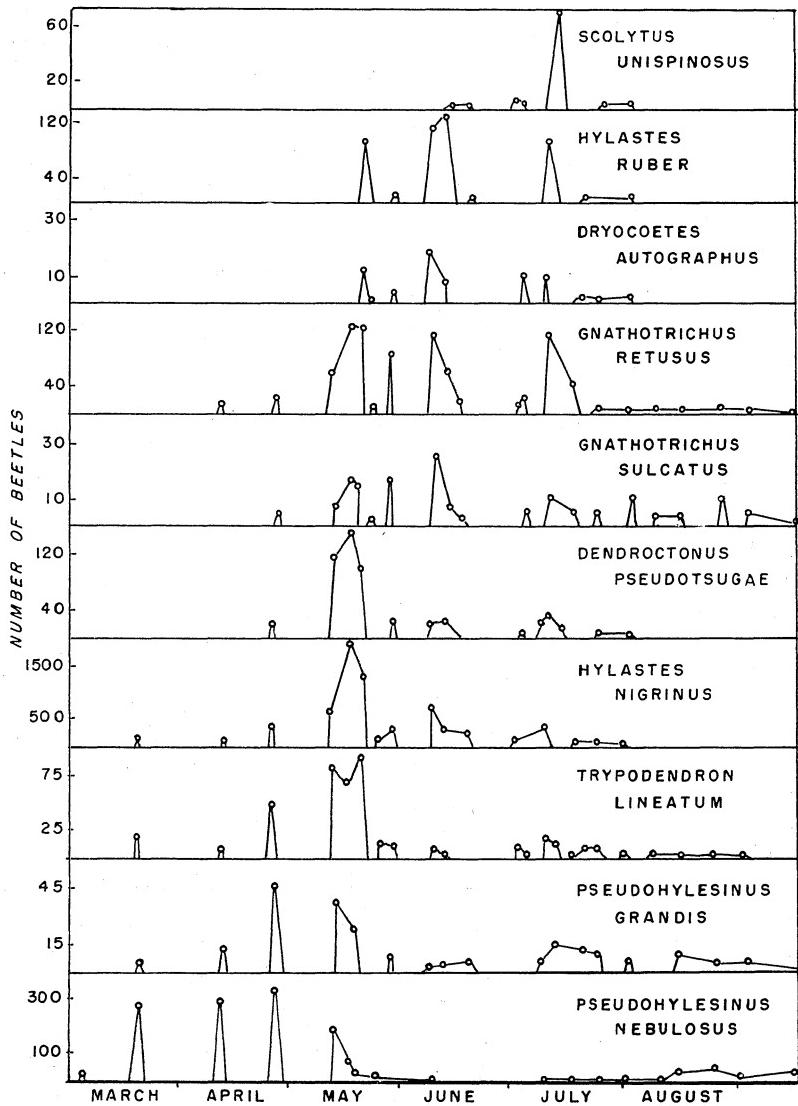


Figure 2. Seasonal flight sequence of scolytid species in 1963.

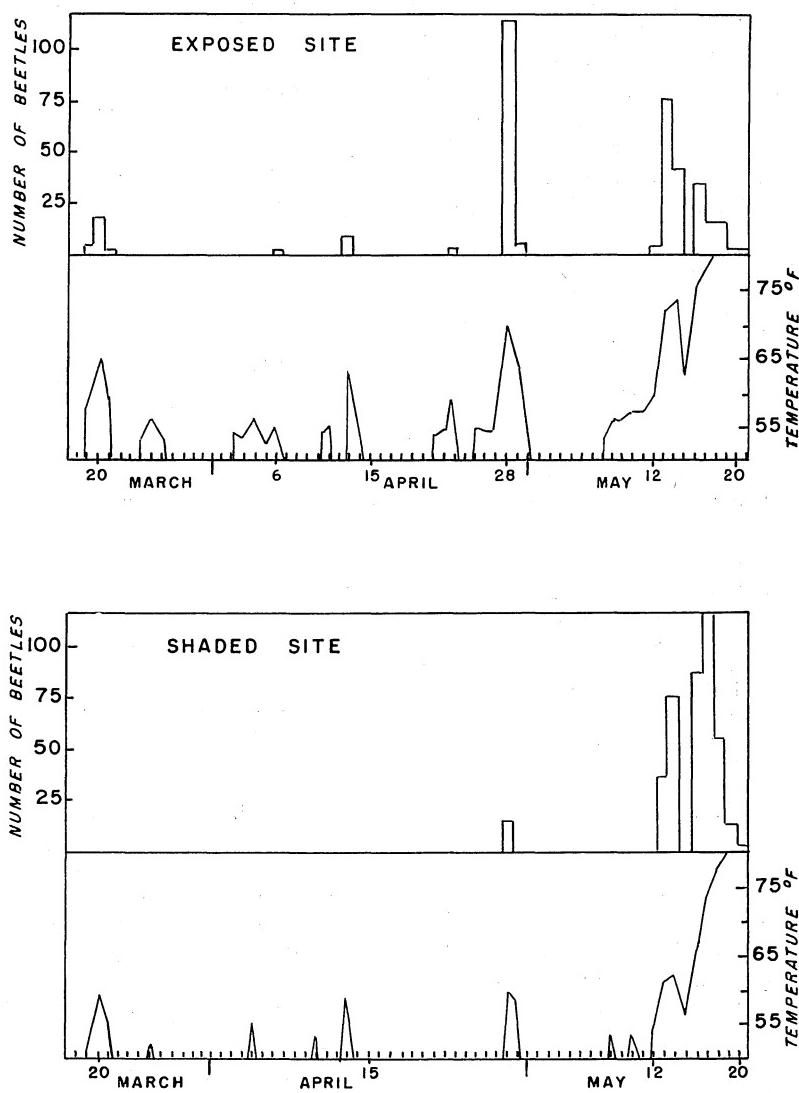


Figure 3. Emergence of *Dendroctonus pseudotsugae* from exposed and shaded sites in relation to maximum daily temperatures in 1963.

plot did not begin until April 28, a difference of 40 days. Since spring activity apparently begins when daily maximum temperatures exceed the activity threshold of the various species, such variations between clearcut and shaded areas can be expected each season, although time difference may vary considerably. For example, during the 1964 season, initial emergence in the clearcut area occurred on March 27 and in the forested area on April 19, a difference of only 23 days. Table 1 provides a comparison of air and subcortical temperatures of logs in the exposed and shaded emergence sites. It is apparent that the inner-bark regions of logs exposed to direct sunlight become much warmer than those protected by the forest canopy, which accelerates development and emergence from logs located in unshaded sites.

Table 1. COMPARISON OF AIR AND BARK TEMPERATURES IN CLEARCUT AND SHADED AREAS, MAY 13, 1963

Hour of day	Clearcut plot		Shaded plot	
	Air temperature °F.	Inner bark temperature °F.	Air temperature °F.	Inner bark temperature °F.
0800	55	48.5	48	44.5
0900	58	61	51	47
1000	60	71.5	53	49
1100	63	75	56	50
1200	66	84	60	52
1300	67	87	60	54
1400	67	86	60	54
1500	68	86	61	54.5
1600	73	84	62	56
1700	69	79	61	55
1730	61	72	59	55

Flight. Temperature was of primary importance also in initiating flight activity. With the exception of *Scolytus unispinosus*, flights were initiated each season as soon as the temperature equalled or exceeded the flight threshold of each species. The flight of the various scolytids was initiated at a wide range of air temperatures, and a sequence of seasonal flight patterns resulted, as shown in Figure 2. Figure 4 illustrates this close relationship of flight activity and maximum temperatures in the family Scolytidae.

Pseudohylesinus Species

Pseudohylesinus nebulosus and *P. grandis* are reported to occur in the Pacific coastal region from British Columbia to California and east into the northern Rocky Mountains (Chamberlin, 1958). *P. nebu-*

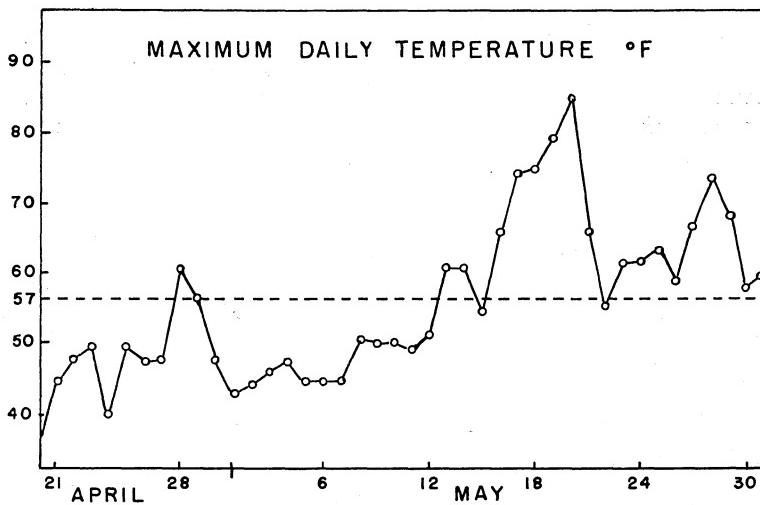
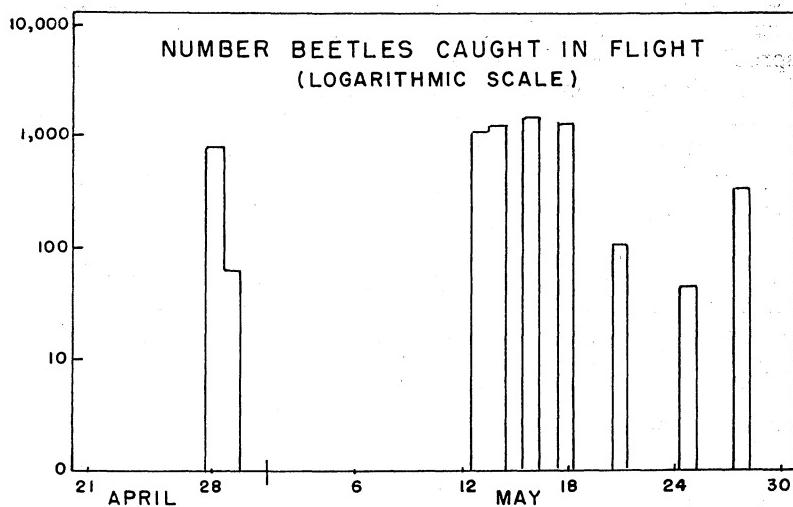


Figure 4. Daily minimum temperatures in relation to the 1963 spring flight pattern of Scolytidae.

losus is primarily found invading Douglas-fir, whereas *P. grandis* also commonly infests grand, white, and silver fir. *P. grandis*, in association with *Pseudohylesinus granulatus*, has recently caused widespread destruction of overmature silver fir stands in Washington. *P. nebulosus* is probably of little economic importance, although Chamberlin (1958) reports that it kills the tops of Douglas-firs and is particularly destructive in small farm woodlots. Walters and McMullen (1956) assert its importance as an interspecific competitor of the Douglas-fir beetle.

P. nebulosus has a one-year life cycle with a single brood per year (Walters and McMullen, 1956). Adults emerge from spring-infested material in late summer, but do not begin a second generation at this time; instead they apparently overwinter in moss, in forest litter, or on tree trunks (Chamberlin, 1939). Therefore, a major attack flight can be expected early in the season, with a subsequent summer flight of new adults to overwintering sites.

P. grandis differs from *P. nebulosus* in that a longer period of time is required for the insect to reach maturity. Thomas and Wright (1961) showed that *P. grandis* has a two-year life cycle in northwestern Washington. Egg galleries and brood are produced by overwintered adults in the spring. The developing larvae overwinter and then mature in midsummer of the following year. The resultant adults do not oviposit immediately, but construct feeding or hibernation galleries in new hosts. One may thus predict a seasonal flight rhythm similar to that of *P. nebulosus*, in that two peaks per season can be expected: an initial attack flight for oviposition in the spring and a summer flight of new adults, matured from the previous year's brood, to feeding or hibernation sites.

Seasonal pattern

Pseudohylesinus nebulosus was the first bark beetle to infest windthrown and fresh-cut timber in 1962, 1963, and 1964, as was also found by Walters and McMullen (1956). In 1963, the initial flight took place on March 20, with peak activity occurring through April 28 (Figure 5). Activity was interrupted for long periods of low temperatures and high precipitation. In 1964, the initial flight occurred about the same time, but the peak of flight activity was over by the end of March. In 1963, the peak of *P. grandis* flight activity occurred from the end of April to mid-May; whereas in 1964, peak activity began in March and continued to mid-May (Figure 7).

The comparatively higher proportion of flight activity of these scolytids in March 1964, can be attributed to a longer period of favorable temperatures than occurred during 1963. Another obvious differ-

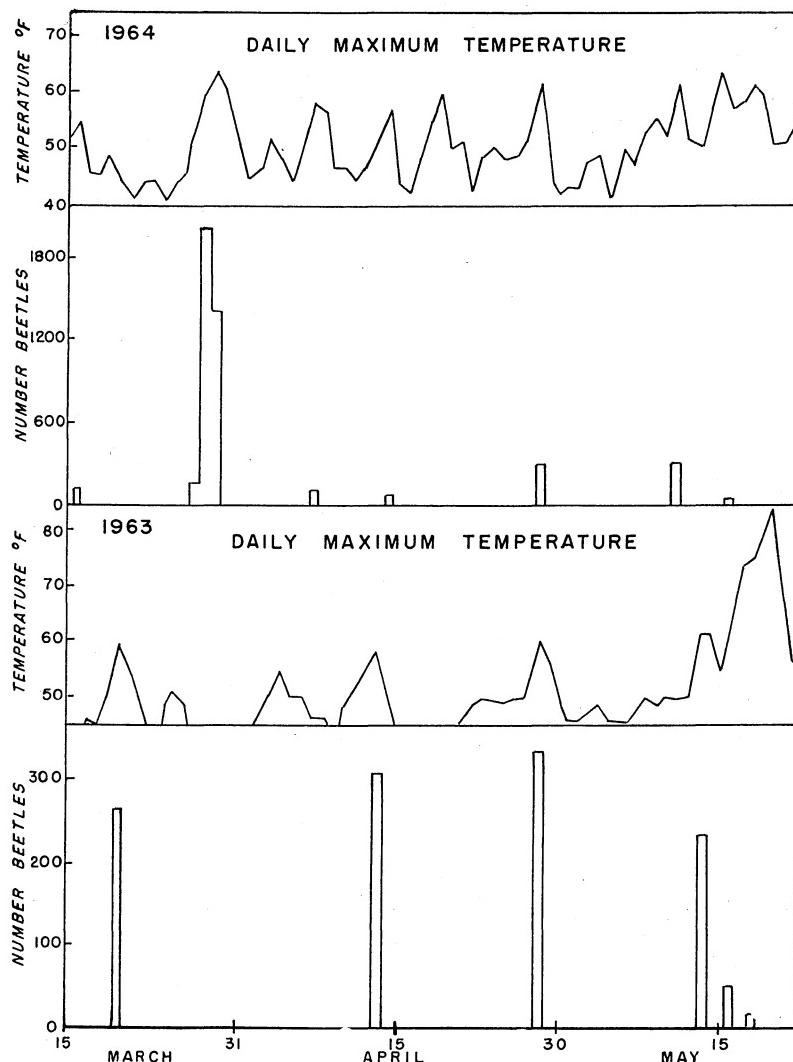


Figure 5. Seasonal flight patterns of *Pseudohylesinus nebulosus* in relation to temperature.

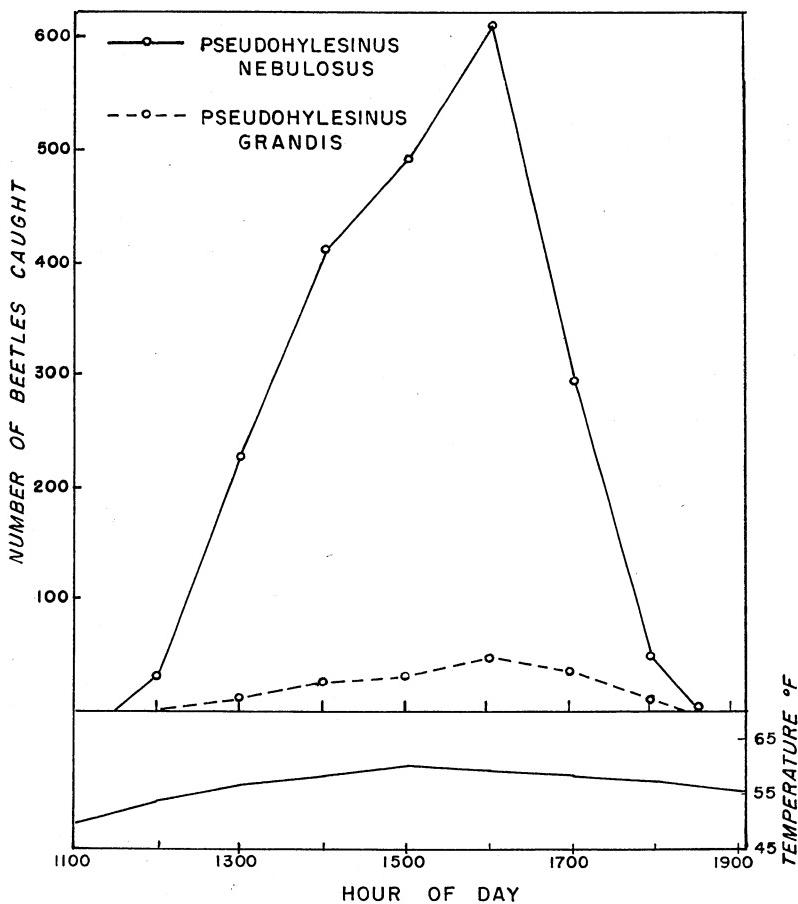


Figure 6. Diurnal flight patterns of *Pseudohylesinus nebulosus* and *P. grandis*.

ence between the two seasons was the higher relative density of *P. nebulosus* beetles in 1964 (Figure 5). The great amounts of wind-thrown timber available in 1963 no doubt contributed to this increase in population. Although the difference in densities of *P. grandis* caught during the two seasons was not nearly as great as for *P. nebulosus*, the number of this species caught in 1964 was considerably higher than in 1963. This increase cannot be attributed to the large amount of suitable host timber available the previous year, however, since *P. grandis* requires two years to complete a single generation.

The low density flights of these scolytids, recorded late in the 1963 season (Figure 2), were composed of new adults flying to winter hibernation quarters. The first *P. nebulosus* callow adults developing from the spring brood were found in the research area on July 26, but the peak of emergence from this material occurred during the latter half of August, and thus corresponded to late-season flight records (Figure 2). The new adults produced a few galleries when supplied with fresh Douglas-fir branches, but these galleries were distorted and no eggs were laid.

The late season phase of *P. grandis* flight occurred in July and August 1963 (Figure 4), which corresponds to the late summer emergence of new adults reported by Thomas and Wright (1961). These individuals had just reached the adult stage after overwintering as larvae the first year of their development. Emergence of *P. grandis* from the caged logs infested in 1962 occurred from August 10, 1963, to September 6, 1963, and corresponded roughly with the late summer flight illustrated in Figure 2. When a number of these emerging adults were provided with fresh Douglas-fir log sections, most of them burrowed into the material, but no eggs were laid and the galleries were small and distorted, an indication that they were probably used only for feeding. This observation substantiates the findings of Thomas and Wright (1961) that new adults of *P. grandis* emerging in late summer do not produce progeny, and that they bore into host material only for feeding or hibernation.

Diurnal pattern

Temperature was the most important factor governing the diurnal activity of these bark beetles. Flight density increased with increasing temperatures and light intensity. However, it is significant that the flight numbers of both species also increased with time, even when temperatures had leveled or decreased slightly (Figure 6).

In 1963, the ambient air temperature necessary to initiate flight of *P. nebulosus* was 54 to 55° F. (Table 2), whereas in 1964 this species was caught in flight at 50 to 51° F. The temperature threshold for flight of *P. grandis* was somewhat higher; the first flights occurred at 56 to 58° F. in 1963 (Figure 6, Tables 3 and 4). These differences in flight temperatures can most likely be attributed to the large amounts of infested windthrow from the October 1962 windstorm which were exposed to direct solar radiation in 1964. It is probable that mature scolytids were able to emerge and fly earlier from hibernation sites in these areas than from cooler, shaded regions within the forest. Once flight has begun it can be sustained through cooler regions (Rudinsky and Vité, 1956; Atkins, 1961). Thus, the 54 to 55° F.

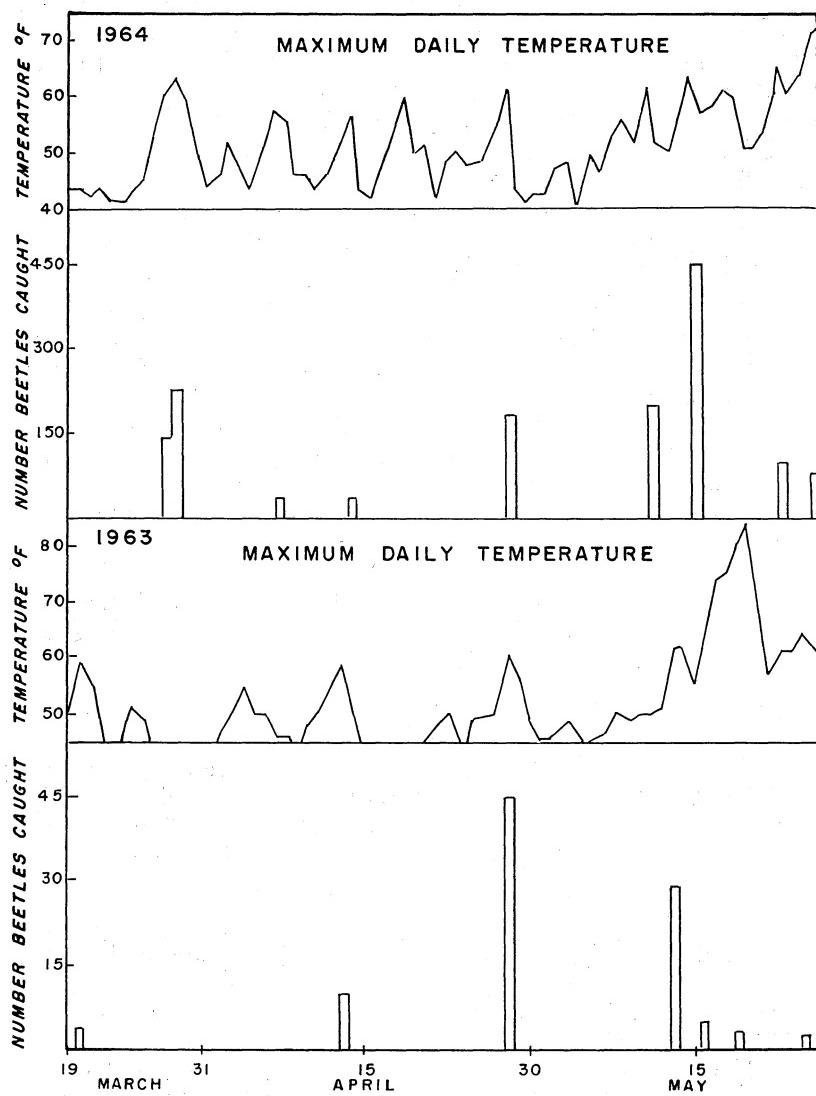


Figure 7. Seasonal flight patterns of *Pseudohylesinus grandis* in relation to temperature.

Table 2. FLIGHT ACTIVITY OF PSEUDOHYLESINUS NEBULOSUS IN RELATION TO DAILY TEMPERATURES IN 1963

Date	Lowest temperature at which initial flight was recorded °F.	Air temperature during hour of maximum flight activity °F.
March 20, 1963	55	58
March 21, 1963	55	56
April 13, 1963	55	58
April 28, 1963	56	60
April 29, 1963	54	56
May 13, 1963	55	61
May 14, 1963	58	63

Table 3. FLIGHT ACTIVITY OF PSEUDOHYLESINUS GRANDIS IN RELATION TO DAILY TEMPERATURES IN 1963

Date	Lowest temperature at which initial flight was recorded °F.	Air temperature during hour of maximum flight activity °F.
April 13, 1963	58	58
April 28, 1963	57	63
April 29, 1963	57	58
May 13, 1963	56	62
May 14, 1963	60	64
May 16, 1963	59	66

temperature threshold found in 1963 for *P. nebulosus* and 56 to 58° F. for *P. grandis* should be regarded as the air temperatures necessary to initiate flight of these species in shaded areas.

It is important to note that a certain intensity of daylight is required for flight to continue. It can be seen from Figure 6 that the flight of *P. nebulosus* decreases sharply when the sun sets, even though the temperature remains favorable. On May 15, 1964, during a period of high flight density, the activity of *P. grandis* began to decrease by

Table 4. DIURNAL FLIGHT OF PSEUDOHYLESINUS GRANDIS IN RELATION TO TEMPERATURE AND TIME OF DAY.

Hour of day	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100
Temp. (°F.)	56	58	58	60	61	63	64	63	63	60	58	57
Beetles caught	0	17	28	68	86	93	91	82	41	30	0	0

1700 hours and had virtually ceased by 1900 hours, although sufficient temperature to support flight prevailed for another two hours (Table 4).

Trypodendron lineatum (Olivier)

Although the ambrosia beetles, woodboring members of the Scolytidae, do not represent a menace to living trees in the Northern Hemisphere, they are well known in the Pacific Northwest because they bore into cut sawlogs, windthrown trees, and other killed timber. Although individually minute, these borings degrade lumber products enough to cause large economic losses each year. *Trypodendron lineatum* appears to be the most damaging of the ambrosia beetles because of its habit of concentrating in dense numbers on host logs. Prebble and Graham (1957) reported gallery densities in excess of 250 per square foot in Douglas-fir logs in British Columbia.

T. lineatum has been reported from Canada, the United States, and northern Europe. Chamberlin (1958) reported that it attacked firs, spruce, pine, hemlock, and Douglas-fir.

T. lineatum has only one generation per year, but a re-emergence of adults later in the season can result in a second brood. Chapman and Kinghorn (1958) observed that spring flight occurred when air temperatures reached 60° F., although small numbers appeared at slightly lower temperatures. Novak (1960) stated that swarms of *T. lineatum* appear when the air temperature reaches 60.8° F., provided that the soil temperature is 46.4 to 50.0° F. Besides re-emerged parent adults, newly emerged adults may also occur in late-season flights. These newly developed adults do not attack hosts at this time; they are in flight to winter hibernation sites.

Chapman (1962) observed that in almost every instance beetles flew against the wind, apparently exhibiting an anemotactic orientation. By utilizing an ingenious array of hidden logs and screening out potential sound and odor production from various controls, Chapman proved that flying *T. lineatum* are drawn toward suitable host logs by attractive odors issuing therefrom. The source of these attractive odors was attributed to the wood tissues or logs *per se*. Recently, however, it has been demonstrated by Rudinsky and Daterman (1964) that the concentration of flying *T. lineatum* on host logs is due to an attractant produced by boring female beetles.

Seasonal pattern

The spring flight of this species was composed of denser populations and was of shorter duration than the late summer flight. In 1963,

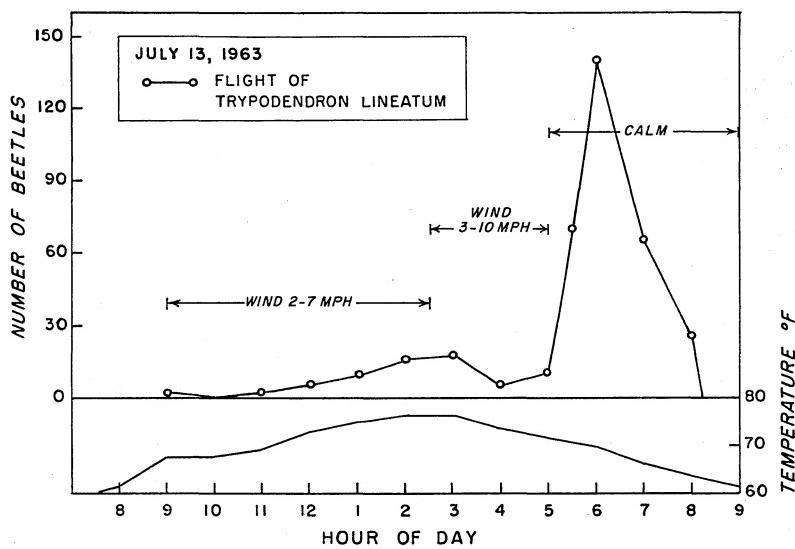


Figure 8. Effect of wind velocity on the flight of *Trypodendron lineatum*.

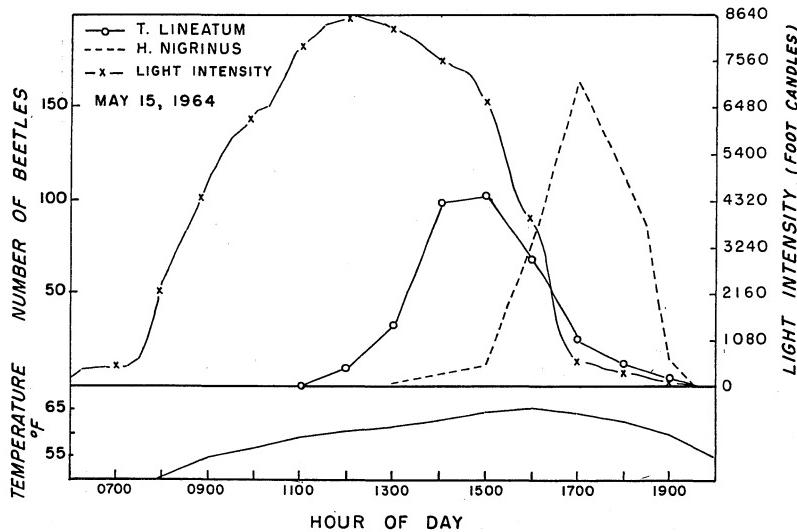


Figure 9. Diurnal flight of *Trypodendron lineatum* and *Hylastes nigrinus* in relation to light and temperature.

spring flight began on March 20, and continued until the last week in May, when activity terminated during a sustained period of warm weather (Figure 10). Although favorable temperatures for flight existed for a number of days in June, very little flight occurred during that time, indicating that the spring emergence and flight of overwintered adults had ceased. In 1964, the spring flight pattern was similar, beginning on March 28 and terminating for the most part by the end of May. Only small numbers of beetles emerged from logs that were infested and caged during the previous season, presumably because most *T. lineatum* emerged from brood logs the previous summer and overwintered in the forest litter.

The late summer phase of flight activity in 1963 began July 3, and was still continuing at a low level when sampling was discontinued on September 24 (Figure 10). The period of highest activity occurred in the first half of July and was probably composed of re-emerging parent beetles. The remaining portion of the curve, extending from July through September, no doubt represents new adults dispersing to hibernation quarters. On July 3, the population in spring-infested logs consisted predominantly of pupae and a few callow adults. This indicated that it was still too early for new adults to be in flight. Emergence from spring-infested material further substantiates the view that the first portion of the late summer flight was composed of re-emerged parent beetles.

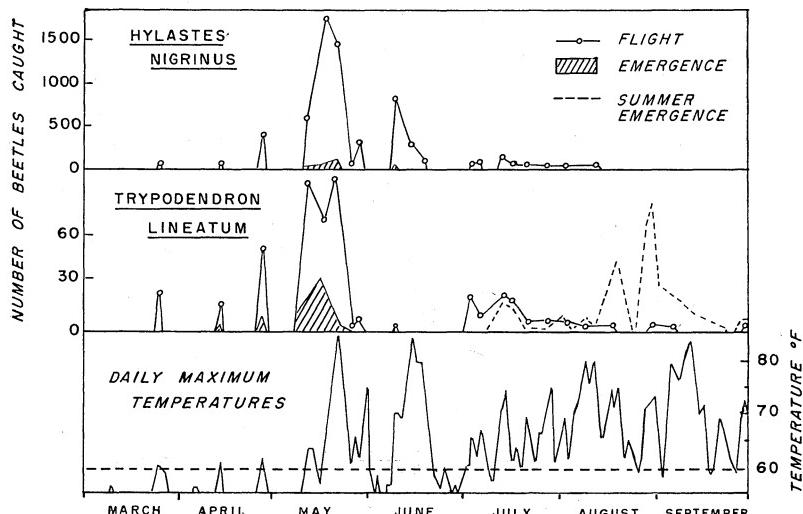


Figure 10. Seasonal pattern of emergence and flight of *Trypodendron lineatum* and *Hylastes nigrinus*.

Figure 10 shows a distinct peak of emergence from these logs in July, representing the re-emerging parents, and this emergence also corresponds roughly with the July flight peak. Emergence then decreased until the middle of August, when a sudden burst of activity occurred and was sustained during favorable weather until mid-September. This late season increase in numbers was apparently composed of matured progeny emerging to fly to winter hibernation sites. It should be noted from Figure 10 that relatively few adults were caught in the nets during August and September in comparison to the large numbers emerging. Possibly this could be because of a lack of sustained flight ability by the new adults. Novak (1960) stated that most new adults emerge and hibernate beneath the brood log in Central Europe, but Kinghorn and Chapman (1959) observed that flight of new adults at this time is typical in British Columbia.

Diurnal pattern

As with the two species of *Pseudohylesinus*, temperature was the primary factor governing the flight activity of *T. lineatum*. Little or no flight occurred in 1963 at ambient air temperatures below 58 to 60° F. (Table 5), corresponding with the flight threshold reported by Chapman and Kinghorn (1958). The few insects caught in flight at lower temperatures were no doubt flying from scattered areas in the forest which were receiving more radiant energy than the research plot. This phenomenon was also seen in the 1964 season when beetles were caught on several occasions at temperatures less than the 58 to 60° F. threshold found in 1963. The cause is believed to be essentially the same as that postulated for *Pseudohylesinus* species since extensive fall and winter logging activity exposed part of the overwintering population to direct solar radiation.

It was observed that daily emergence began at somewhat lower temperatures than flight. Beetles were found emerging at inner-bark

Table 5. FLIGHT ACTIVITY OF TRYPODENDRON LINEATUM IN RELATION TO DAILY TEMPERATURES IN 1963

Date	Lowest temperature at which initial flight was recorded	Air temperature during hour of maximum flight activity
March 20, 1963	59	59
April 13, 1963	58	59
April 28, 1963	59	62.5
May 13, 1963	60	64
May 14, 1963	61	65
May 16, 1963	60.5	66

temperatures of 50 to 52° F., provided that the air temperature was 56° F. or more. This finding differs somewhat from Novak's report (1960, p. 17) that a ground-litter temperature of 46.4 to 50.0° F. was necessary for emergence.

A decrease in flight was noted in the evening hours with decreasing light intensity, even though the temperature remained favorable (Figure 9).

Olfactory response

Trypodendron lineatum exhibited a definite olfactory response to certain infested logs, with a profound effect on local flight density. During the first few days of flight in 1963, no particular difference was noticed in the numbers of insects caught in the six sampling nets. Then the windthrown logs near Net 1 were infested on April 28. The attractant produced by these invading beetles caused a striking increase in local flight activity and resulted in exceptionally high catches of beetles in Net 1 on subsequent days of flight (Table 6). Since the duration of effectiveness of this attractant is not known, the numbers of *T. lineatum* caught in Net 1 were not used in reconstructing the seasonal flight pattern in Figure 10. A seasonal pattern based on the numbers caught in the remaining five nets was thought to be more representative of the activity of this species.

Table 6 also shows that somewhat higher numbers of *T. lineatum* were caught at Nets 2 and 3, which were located near uninjected host material, than at Nets 4, 5, and 6, which were not near a suitable host. These figures may indicate that the insects are attracted by the host *per se*; however, the difference in numbers caught in Nets 2-6 might be due to factors other than host attraction, such as the degree of canopy shade, topographical position, density of the surrounding understory, or position in regard to prevailing air currents. It is apparent that knowledge of bark-beetle flight behavior and proficiency in bark-beetle flight sampling can be increased by critical studies of host attraction and effects of sampling position on sampling efficiency.

Effect of wind

The olfactory studies of this species (Rudinsky and Daterman, 1964) enabled a more accurate observation of the effect of varied wind velocity on beetle flight. Sampling by nets proved to be less than successful for this purpose, since only low numbers of scolytids were in flight when adverse wind conditions were present for testing, and because steady winds of even low velocities caused very sharp decreases in the number caught. The effect of varying wind velocities on numbers of *T. lineatum* caught in an olfactory cage containing a female-infested log (Rudinsky and Daterman, 1964) is shown in

Table 6. NUMBERS OF TRYPODENDRON LINEATUM TRAPPED AT VARIOUS NET LOCATIONS DURING 1963 IN RELATION TO THE PROXIMITY OF INFESTED AND UNINFESTED HOST LOGS.

	Seven yards from logs infested April 28, 1963	Ten and five yards respectively from log uninsected in spring flight		Twenty-five yards or more away from suitable host logs		
Date	Net 1	Net 2	Net 3	Net 4	Net 5	Net 6
April 13	2	---	3	0	0	---
April 28	28	10	21	4	7	8
May 13	113	20	25	14	10	10
May 14	160	19	29	4	9	2
May 16	236	18	26	5	6	5
May 18	150	7	10	6	13	55 ¹
May 19	21	2	3	0	1	3
May 21	8	1	1	0	1	1
May 28	7	0	4	0	0	1
Totals	725	77	122	33	47	85

¹ This comparatively large number may have been due to a possible attraction caused by a Douglas-fir tree felled May 17, 1963, and cut into sections on May 18, 1963.

Figure 8. While it is obvious that wind exerts an adverse effect on flight activity, flight is not terminated by the velocities shown in Figure 9. With winds of these velocities, flight apparently is more sporadic and probably occurs at lower heights where wind speed is somewhat slowed by the forest undergrowth.

***Hylastes nigrinus* (Mannerheim)**

Relatively little information is available on the biology or general life history of *Hylastes nigrinus*. It has been found infesting the roots of stumps and dying Douglas-fir trees, and Chamberlin (1958) reported attacks on the roots of living trees. Recently it has been shown that *H. nigrinus* also infests boles of windthrown Douglas-fir. Over 90 individuals of *H. nigrinus* were recorded emerging within a period of two days in 1962 from logs that had been invaded as fresh wind-thrown the previous year. Apparently no economic damage to standing timber has been traced to this insect. Besides Douglas-fir, *H. nigrinus* has also been reported infesting western white pine and western hemlock. Its range is reported by Chamberlin (1958) as the Northwest, extending into the Yukon, California, and the Rocky Mountains.

Certain information concerning the flight patterns of *H. nigrinus* is provided by Gara and Vité (1962). *Hylastes macer* and *Hylastes minutus* were also present in the California pine forest where these workers conducted their research, and the activities of the three species were considered together under the generic name *Hylastes*. Seasonal flight began in April and terminated in May in that northern California location. In addition, it was reported that the genus had a consistent diurnal flight pattern with peak activity occurring at about 1800 hours in the evening. This finding was corroborated in the present study.

Seasonal pattern

Like *Trypodendron lineatum*, the spring flight of *H. nigrinus* began in March. Unlike *Trypodendron* or *Pseudohylesinus* species, activity did not cease during the first extensive period of warm weather in May, but continued for a longer period of time (Figure 10). Small numbers of this species were found emerging in April and May of 1963 from caged Douglas-fir windthrow infested the previous year (Figure 10), but the numbers emerging were too few for observations regarding the effects of temperature or other factors.

Diurnal pattern

Very few of this species were caught in flight on days when ambient air temperatures were below 58 to 60° F. (Table 7). While this temperature range is probably close to the threshold necessary to initiate flight, it was found that large numbers of this species did not

Table 7. FLIGHT ACTIVITY OF *HYLASTES NIGRINUS* IN RELATION TO VARIOUS PHYSICAL FACTORS IN 1963

Date	Time maximum flight occurred	Temp.	Percent of relative humidity	Apparent condition of light intensity	Temperature condition the following hour	Temperature at which initial flight occurred
April 28	1700	60.5	58	Decreasing	Below threshold	58
May 13	1600	62	43	Decreasing	Below threshold	60
May 14	1300	64	60	Low (overcast)	Below threshold	61
May 16	1730	63	52	Decreasing	Optimal	62
May 18	1730	66	38	Decreasing	Optimal	62.5
May 19	1900	75	32	Very low	Optimal
May 21	1600	64	66	Decreasing	Below threshold	60
May 28	1730	65	46	Decreasing	Optimal	64
June 10	1730	66	60	Decreasing	Optimal	65
June 13	1830	70	53	Decreasing	Optimal
June 17	1830	69	58	Decreasing	Optimal

appear in flight except on days when maximum temperatures reached 64° F. or more (Figures 11 and 12). Such behavior differs from that observed for the species previously discussed. This difference exhibited by *H. nigrinus* is apparently due to a strong influence exerted by light intensity.

This bark beetle can be classified as crepuscular in its daily flight rhythm since its activity occurs primarily during the late afternoon or early evening hours. Figure 9 and Table 7 present the time of flight characteristic of this species. It can be seen that little flight occurs during mid-day even though the temperature is favorable (Figures 9, 11, 12, Table 7). This explains why so few of these insects are found in flight on days when the temperature just equals or barely exceeds the assumed threshold of 58 to 60° F.

The strong influence of light intensity upon the flight activity of this species is exemplified by the diurnal activity pattern on May 14, 1963 (Table 7). A cloud formation resulting in a completely overcast sky by 1215 hours caused a distinct decrease of light intensity in the forest. Subsequent net collections at 1300 hours revealed a sharp increase in numbers of *H. nigrinus* in flight. At 1200 hours, 99 specimens were collected, whereas 832 were trapped in the nets during the following hour. It is significant to note that air temperature remained stable at 64° F. from 1100 hours until 1305 hours. On May

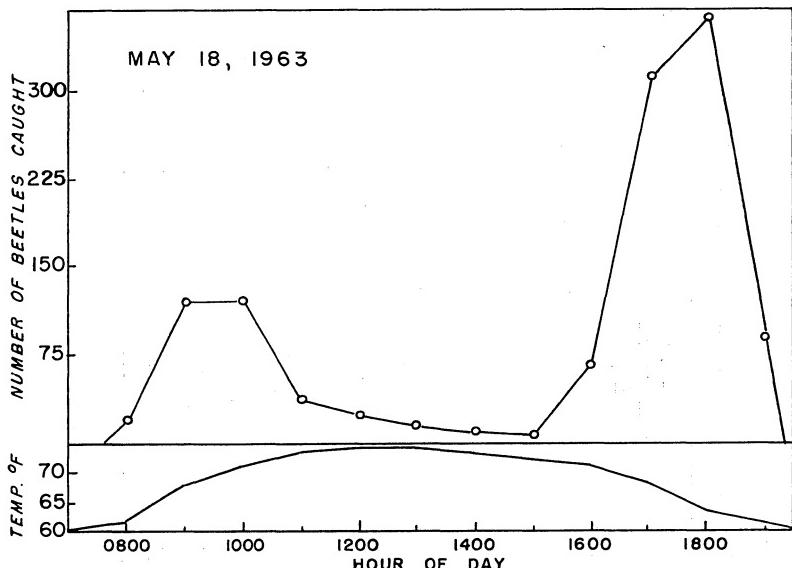


Figure 11. Flight of *Hylastes nigrinus* with high temperatures.

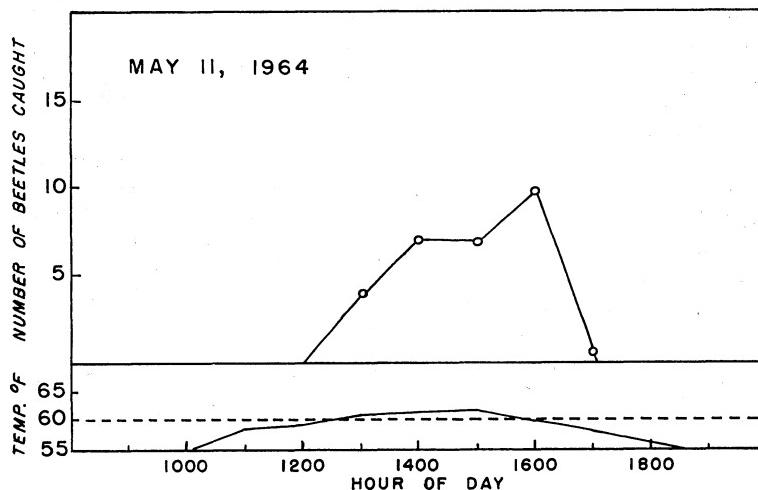


Figure 12. Flight of *Hylastes nigrinus* with marginal temperatures.

18, 1963, when favorable temperatures prevailed throughout the entire day, a morning flight period was observed in addition to the usual late afternoon activity (Figure 11). This observation further indicates the importance of light intensity as a factor determining the time of daily flight activity.

For a brief period in 1964, more exact information was obtained through use of the illuminometer for measurement of light intensity. Figure 11 depicts the daily curve of light intensity in relation to the flights of *Trypodendron lineatum* and *H. nigrinus*. Light intensities below 500 foot-candles are apparently most favorable for *H. nigrinus* flight activity. During intermittent overcast periods, the illuminometer recorded light intensities as low as 850 foot-candles. This figure is sufficiently low to explain the marked increase in flight of *H. nigrinus* during heavy overcast periods such as May 14, 1963 (Table 7). The illuminometer was located in a relatively unshaded position, and probably recorded the maximum light intensity in the research area; actual light intensities existent in the various bark-beetle microhabitats from which flights were initiated would likely be considerably lower. Thus the most favorable light intensity for a crepuscular species like *H. nigrinus* might be less than 100 foot-candles. Controlled laboratory experiments would, of course, be necessary to prove this assumption.

It may also be significant that excessive temperatures can have a delaying effect on the usual pattern of daily flight. On May 19 and June 13 and 17, 1963 (Table 7), prevailing temperatures were considerably higher than usual and maximum flight activity occurred at a

later hour. This was particularly evident on May 19, when peak flight occurred at 1900 hours. On this date, maximum activity occurred at a temperature of 75° F., and temperatures of 77 to 79° F. prevailed until 1800 hours. It is possible that temperatures above 75° F. are inhibitory to *H. nigrinus* flight.

Extremes of relative humidity and changes in relative humidity were also considered as possible factors which might affect crepuscular flight patterns. However, no correlation with flight was found at the relative humidity conditions that occurred during these studies.

***Gnathotrichus* Species**

Gnathotrichus retusus and *G. sulcatus* were two other species of ambrosia beetles commonly found flying in the study area. Less information is available on the biology and flight habits of these species than on *T. lineatum*. Chamberlin (1958) reported that *G. retusus* is common in the Pacific Northwest and ranges from British Columbia to California, and east to Nevada and South Dakota. He reported *G. retusus* infesting ponderosa, jeffrey, lodgepole, western white, sugar, and Monterrey pines, grand and red firs, Douglas-fir, and western hemlock. *G. sulcatus* was reported to have a similar distribution, and Chamberlin stated that this species probably attacks any conifer within its range.

Chapman and Kinghorn (1958), treating the two species as one, stated that the seasonal flight pattern of *Gnathotrichus* is clearly different from that of *Trypodendron*. Graphic illustration by these workers showed a low density flight of the two species occurring throughout the summer with two distinct peaks of activity; the first peak occurred in late June and July and the second in September. Prebble and Graham (1957) reported that *G. sulcatus* is commonly in flight one or two weeks later in the spring than *Trypodendron*, with a second wave of attacks occurring in late summer or autumn.

In the present study, no appreciable differences were noted between the flight patterns of *Gnathotrichus retusus* and *G. sulcatus*, and the two species are discussed together.

Seasonal pattern

Gnathotrichus species began seasonal activity at about the same time as the Douglas-fir beetle. Considerable numbers of these ambrosia beetles continued to fly throughout the summer (Figure 13). Low numbers were recorded flying in April, with maximum activity occurring in May and June.

Since much of the life history of these insects is unknown, it was impossible to define the seasonal flight pattern in terms of the origin of beetles in flight during the season. Although *Gnathotrichus*

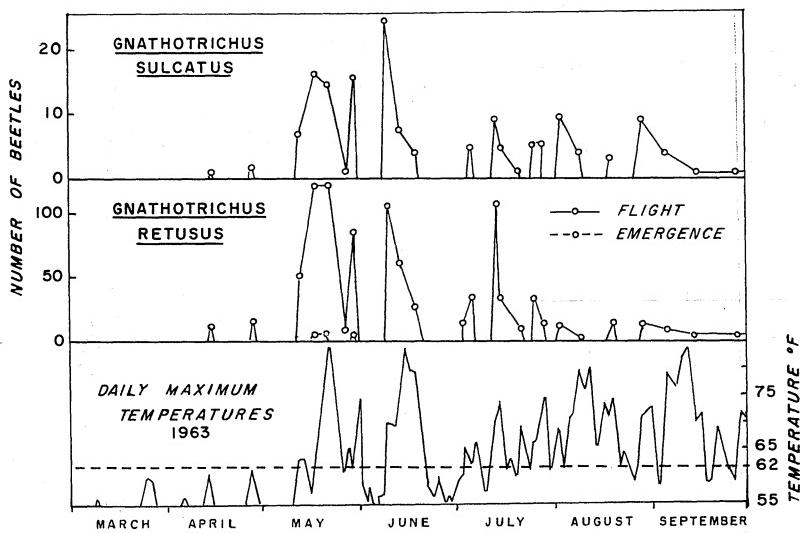


Figure 13. Seasonal flight of *Gnathotrichus sulcatus* and *G. retusus* in 1963.

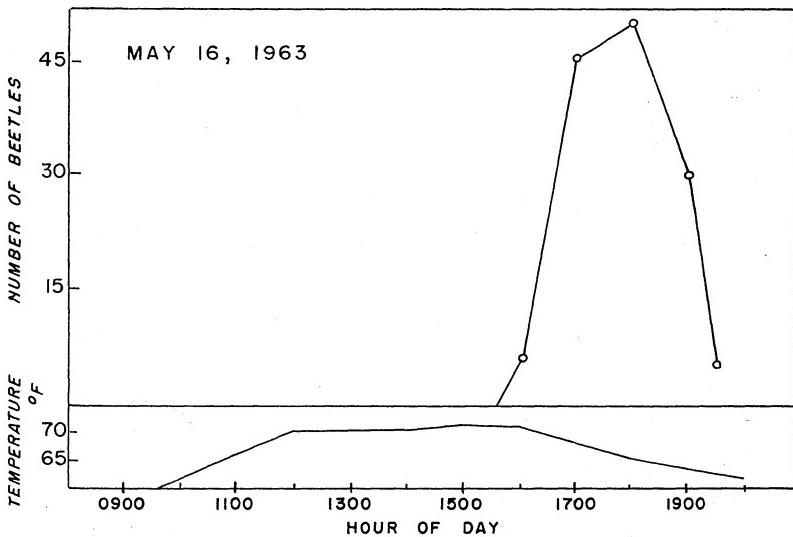


Figure 14. Flight of *Gnathotrichus* species in clear weather.

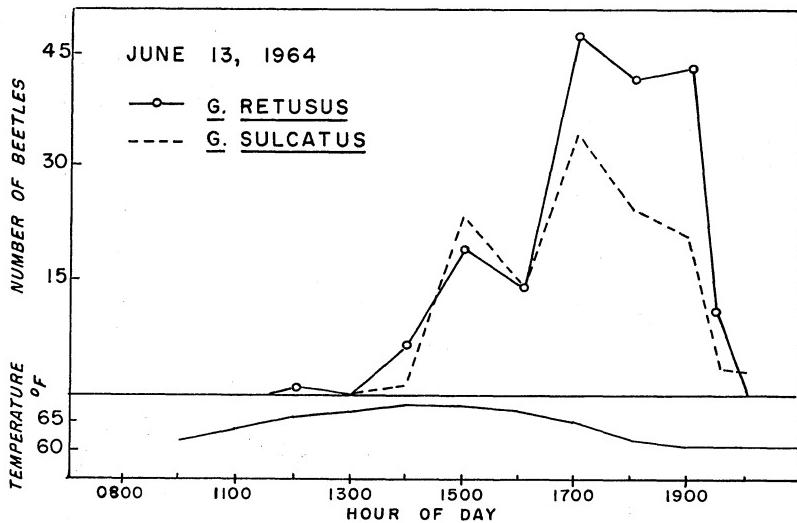


Figure 15. Flight of *Gnathotrichus retusus* and *G. sulcatus* in overcast weather.

emerging from logs infested the previous year were low in number, all had emerged by the second week in June. This is perhaps an indication that dispersal of overwintered adults had ceased by this time, and subsequent activity was due to re-emerged parent beetles.

Diurnal pattern

Temperature was important in governing flight, but light intensity was of primary influence in the timing of daily maximum activity. Like *Hylastes nigrinus*, *Gnathotrichus* species exhibited a crepuscular pattern of flight. During clear weather, low numbers were first caught in mid-afternoon, with maximum activity occurring about 1800 hours. With favorable temperatures, sporadic flight was recorded earlier on intermittently cloudy days such as May 14, 1963 (Table 8), and flight at low densities occurred through the duration of heavily overcast days (Figure 15).

The influence of light intensity was generally similar but somewhat more restricted than that observed for *H. nigrinus*, and an interrelation of light and temperature was noted in the timing of the daily flight rhythm. It can be observed from Table 8 that on occasions when maximum flight occurred before 1730 hours, activity was depressed or terminated by temperatures below the minimal level. On occasions when the temperature remained higher, flight peaks occurred between 1730 and 1830 hours (Table 8). Since the time of maximum evening activity was somewhat later for *Gnathotrichus*

Table 8. FLIGHT OF *GNATHOTRICHUS* SPECIES IN RELATION TO TEMPERATURE AND THE TIME OF DAY FOR 1963

Date	Hour of day maximum flight occurred	Temperature	Temperature condition the following hour	Condition of light intensity	Temperature at which initial flight occurred
°F.					
May 13	1600	63	Below threshold	Decreasing	61
May 14	1330	62	Below threshold	Low (overcast)	64
May 16	1730	63	Marginal	Decreasing	65
May 18	1800	65	Optimal	Decreasing	72
May 19	1830	77	Optimal	Decreasing
May 25	1600	63	Below threshold	Decreasing	63
May 28	1730	65	Below threshold	Decreasing	63
June 10	1730	66	Optimal	Decreasing	68
June 13	1830	70	Optimal	Decreasing	72
June 17	1800	71	Optimal	Decreasing
July 12	1800	70	Optimal	Decreasing
July 13	1800	70	Optimal	Decreasing	64
July 25	1800	65	Optimal	Decreasing	63

species than for *H. nigrinus*, it is probable that a lower range of light intensity is more favorable for flights of these scolytids. In contrast to *H. nigrinus*, no early morning flight of *Gnathotrichus* was recorded, but such a phenomenon could perhaps occur. Indeed, flights recorded on overcast days (Table 8, Figure 15) are evidence that such activity could occur with temperatures of at least 61 to 63° F.

Temperature preferences for these two species apparently differ little, since the beetles were usually caught in the same relative densities under identical temperature conditions. Although it is difficult to determine threshold flight temperatures for these species since their flight begins late in the day when the temperature may have passed the threshold, it is nevertheless evident from Table 8 that maximum activity was recorded on days when air temperature reached 65° F. or higher. Lower numbers of beetles were caught in flight when temperatures were 61 to 63° F., which can be regarded as close to the flight threshold.

Too few specimens of this genus emerged from caged material to establish any definite air or bark temperatures required for emergence.

***Dryocoetes autographus* (Ratzeburg)**

In a recent revision of this group, Bright (1963) listed *Dryocoetes americanus* Hopkins, *D. septentrionis* LeConte, and *D. pseudotsugae* Swaine as synonymous with *D. autographus*. The geographic range of this insect extends throughout the coniferous forests of Europe and Asia, and in North America north of New Mexico and North Carolina. Bright (1963) listed spruce, hemlock, and Douglas-fir as the main groups of host trees. Chamberlin (1958), discussing *D. septentrionis*, concluded that it is of little economic importance since it seldom attacks living trees. Although the species is probably not a forest pest, it may have some importance as an interspecific competitor of the Douglas-fir beetle for gallery space within available host material.

Seasonal pattern

This insect was found to fly later in the season than the species discussed above, apparently because higher temperatures are essential for its dispersal activity. As illustrated in Figure 16, all phases of the seasonal pattern correspond with the periods of higher temperatures which occurred sporadically during 1963. It is unlikely that this late-season pattern results from the insect's overwintering in an immature stage, because overwintering adults were found when the logs used in the 1963 season were examined in January. Neither emergence nor flight activity occurred before mid-May (Figure 16). Maximum flight

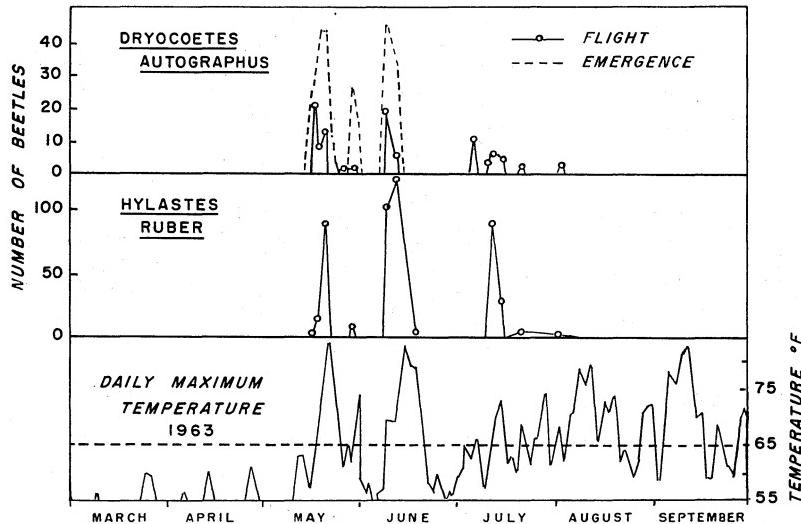


Figure 16. Seasonal activity patterns of *Dryocoetus autographus* and *Hylastes ruber* in 1963.

took place in May and June, with some interruptions by cool weather. Low numbers of this species also flew in July and August. These late flyers may have been re-emerged adults, but probably represented an extension of the initial dispersal flight that was delayed by a prolonged period of cold weather in late June and part of July.

Diurnal pattern

D. autographus was found to have a crepuscular flight pattern, similar to that described for *Gnathotrichus* species and *Hylastes nigrinus*, with initiation of flight consistently occurring just before or during the twilight hours. On various sampling days from May 16 to July 13, 1963, maximum flight occurred between 1700 and 1900 hours (Table 9). This represents a somewhat wider range of favorable twilight hours than that observed for *Gnathotrichus* species. *D. autographus* also flew earlier on days when light intensity was decreased by overcast weather conditions. Figure 18 illustrates the longer period of daily activity usually occurring with overcast skies, whereas Figure 17 depicts the typical crepuscular rhythm associated with clear weather.

Because of the evening flight habits of this insect and the low numbers caught in flight, it was difficult to establish the temperature thresholds of emergence and flight activity. However, some indication of temperature preferences for flight activity is obtainable from the data summarized in Table 9. It is probable that the air temperature

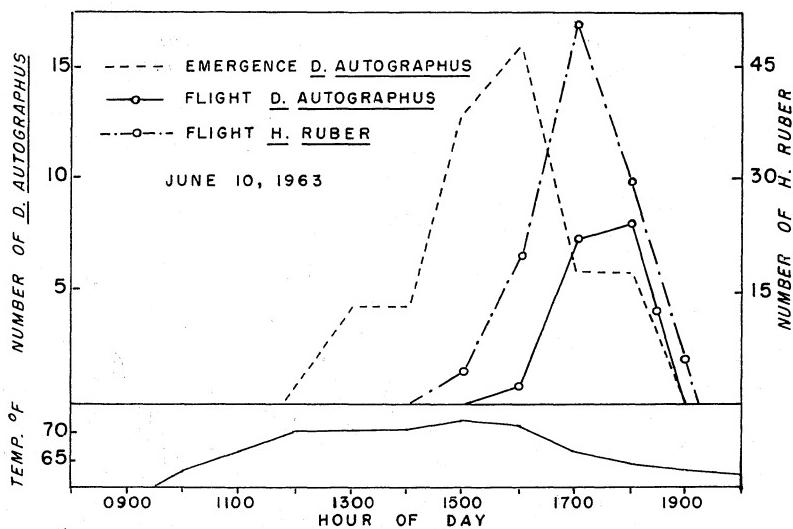


Figure 17. Flight of *Dryocoetes autographus* and *Hylastes ruber* in clear weather.

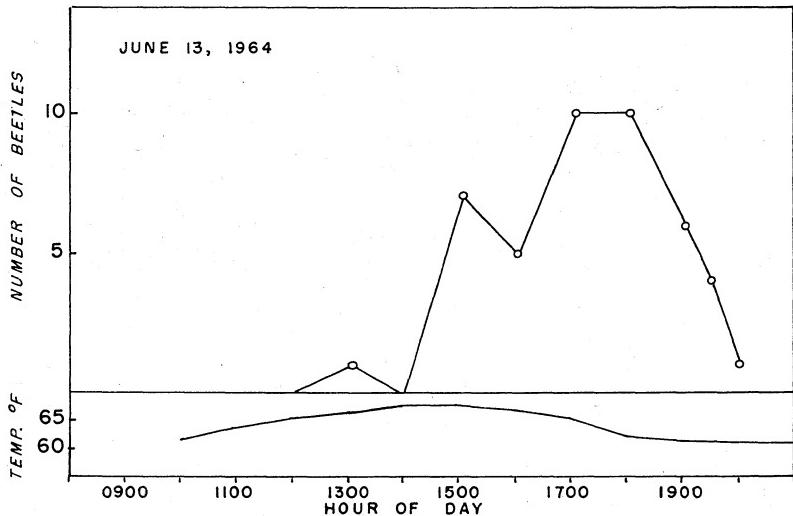


Figure 18. Flight of *Dryocoetes autographus* in overcast weather.

necessary to initiate flight activity of *D. autographus* lies between 65 to 68° F. However, once flight has begun, it can be sustained at temperatures somewhat lower than 65° F.

This species differed somewhat from *Trypodendron lineatum* and other species studied, in that emergence did not occur at temperatures lower than those necessary to support flight activity. On 12 days when emergence was recorded from the shaded cage, no emergence took place when air temperatures were below 66° F.

***Hylastes ruber* Swaine**

Little information is available regarding the biology of *Hylastes ruber*, and apparently no significant economic damage has been traced to it. According to Chamberlin (1958), *H. ruber* is somewhat more confined in its distribution than *H. nigrinus*, and is reported from British Columbia, Washington, and Oregon. Douglas-fir is the only reported host.

Seasonal pattern

Hylastes ruber, like *Dryocoetes autographus*, demonstrated a dependency on higher temperatures for initiation of dispersal flights. In 1963, the seasonal activity of this bark beetle began May 18, coinciding with the beginning of the *Dryocoetes* flight. A relatively greater amount of activity by this species took place in June and July, as compared with *Dryocoetes* (Figure 16). Because information is unavailable on the life history of this species, it is questionable whether the occurrence of initial seasonal activity depended entirely on a temperature threshold. It is significant that no seasonal flight by this insect was recorded prior to the first period of fair weather and higher temperatures in mid-May. This close relationship of flight activity with sporadic periods of high temperatures (Figure 16) seems to indicate that temperature is the primary factor regulating flight.

Diurnal pattern

Substantial flight of this scolytid took place on only a few days, so only limited data on dispersal activity are available.

It is evident from Table 10 and Figure 17 that higher temperatures than the thresholds found for species discussed earlier are necessary to initiate the flight activity of *H. ruber*. Air temperatures of at least 68° F. are apparently necessary to induce flight.

Hylastes ruber was the fifth species found to have a crepuscular flight pattern. This species, like *Hylastes nigrinus*, flew consistently during the early evening hours (Figure 17). Maximum flight occurred between 1700 and 1830 hours (Table 10), and it is probable that light intensities recorded as most favorable for other crepuscular

Table 9. FLIGHT OF DRYOCOETES AUTOGRAPHUS IN RELATION TO TEMPERATURE AND THE TIME OF DAY IN 1963

Day	Hour of day maximum flight occurred	Temp.	Temperature condition the following hour	Condition of light intensity	Temperature at which initial flight occurred
		°F.			°F.
May 16	1700	65	Below threshold	Decreasing	68
May 18	1700	68	Optimal	Decreasing	71
May 19	1830	77	Optimal	Decreasing	78
June 10	1730	65	Below threshold	Decreasing	68
June 13	1800	71	Optimal	Decreasing	75
July 5	1700	63	Below threshold	Decreasing	66
July 11	1700	64	Below threshold	Decreasing	66
July 12	1830	70	Optimal	Decreasing	71.5
July 13	1900	68	Optimal	Decreasing	68

Table 10. FLIGHT OF HYLASTES RUBER IN RELATION TO TEMPERATURE AND THE TIME OF DAY IN 1963

Date	Hour of day maximum flight occurred	Temp.	Temperature condition the following hour	Condition of light intensity	Temperature at which initial flight occurred
		°F.			°F.
May 18	1730	67	Below threshold	Decreasing	68
May 19	1830	77	Optimal	Decreasing	78
June 10	1700	67	Below threshold	Decreasing	70
June 13	1800	72	Optimal	Decreasing	73
July 12	1730	71	Optimal	Decreasing	73
July 13	1800	71	Optimal	Decreasing	74

species would also be optimal for this scolytid. While an early morning pattern of flight was not uncommon with *Hylastes nigrinus*, it is unlikely to occur with *H. ruber* in the coastal forests of the Pacific Northwest because temperatures are usually low early in the day.

***Scolytus unispinosus* LeConte**

Scolytus unispinosus has been reported as an occasional killer of young Douglas-fir trees by Chamberlin (1958). McMullen and Atkins (1962) stated that the species is of minor economic importance, usually confining its attack to tops and limbs of trees killed or severely damaged by other agents. According to these authors, the species is common throughout the Pacific coast and Rocky Mountain regions. The principal host is Douglas-fir.

McMullen and Atkins (1962) found that weather conditions have a marked effect on the development and flight of *S. unispinosus*. Overwintering occurs primarily as fourth-instar larvae, and a single generation and brood are produced annually in the interior of British Columbia. During three years of studying this species in British Columbia, McMullen and Atkins observed a wide variation in seasonal flight periods according to the weather: In 1958 the peak activity occurred in the latter part of May, in 1959 in early June, and in 1960 in late June. These authors found that the species was seldom caught in flight when the temperature was below 68 to 70° F.

Seasonal pattern

The seasonal flight of *Scolytus unispinosus* was of short duration and was composed of relatively low numbers. Therefore, it was somewhat difficult to assess the effects of the various physical factors.

This beetle is exceptional among the scolytids treated here in that its seasonal flight did not begin with the initial occurrence of favorable temperatures. This is not surprising, however, since it overwinters in the third and fourth larval stages and a sufficient period of favorable temperature must occur during the spring for brood maturation. After development to the adult stage, dispersal flights occurred with favorable temperature.

Emergence from caged host material infested by this insect did not occur in the shaded area until June 1963, and maximum emergence did not occur until mid-July (Figure 19). These logs had been examined the second week of April and found to contain only late instar larvae. Emergence of this species from the cage exposed in the clear-cut area of the forest occurred considerably earlier (Figure 19). Peak activity was recorded at the exposed position about June 10, and at the shaded plot on July 12, 1963.

In 1963, no flight of this scolytid was recorded in May and little in June, even though considerable periods of favorable weather occurred within this time (Figure 19). In July, however, these insects had matured and were ready to fly with the first occurrence of favorable conditions. In 1964, large numbers of this scolytid were recorded in flight as early as June 22. As shown in 1963 and 1964, it appears that late June and early July is the most likely period for flights of this bark beetle.

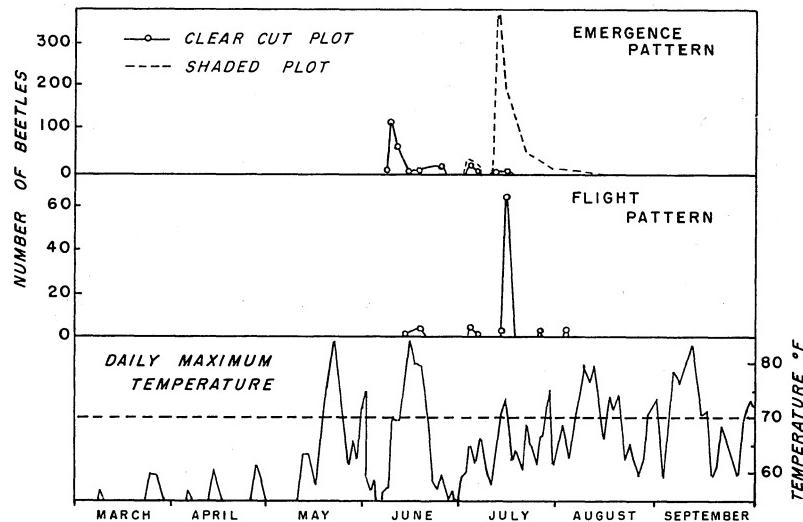


Figure 19. Seasonal emergence and flight activity of *Scolytus unispinosus* in 1963.

Table 11. FLIGHT ACTIVITY OF SCOLYTUS UNISPINOSUS IN RELATION TO DAILY TEMPERATURES IN 1963

Date	Lowest temperature at which initial flight was recorded	Air temperature at hour of maximum flight activity
	°F.	°F.
June 17, 1963	72	78
July 3, 1963	69	69
July 12, 1963	71	74
July 13, 1963	75	78
July 25, 1963	68	69
August 2, 1963	75	75

Diurnal pattern

Scolytus unispinosus exhibited a mid-day or early afternoon diurnal flight rhythm like that of *Pseudohylesinus* species, *Trypodendron lineatum*, and *Dendroctonus pseudotsugae* (Figure 21). Considerably higher temperatures were required to support the flight of this species than were found necessary for the others. It is evident from Table 11 that air temperatures in excess of 70° F. are most favorable for dispersal activity, and it is probable that the threshold air temperature necessary to initiate the flight of this scolytid is within the range of 68 to 72° F. Emergence was found to begin at somewhat lower temperatures than those necessary for flight. On at least two occasions, daily emergence began at air temperatures as low as 65 to 66° F.

The flying population decreased sharply in the late afternoon, even though temperatures remained favorable. This behavior is exemplified on July 13, 1963 (Figure 21), when activity decreased sharply at 1600 hours, although temperature remained above 70° F. past 1800 hours. This depression effect may be due to the normal decrease in light intensity; however, exact determination of the cause of such responses requires study under controlled conditions.

Miscellaneous Species

In both 1963 and 1964, a number of other bark beetles species were caught in addition to those discussed above. Most of these were present in too small numbers to permit reliable interpretation of the effects of the physical factors on flight activity. Table 12 lists the less abundant species in the sequence in which they were caught during the season. A greater number of *Phloeosinus* species were caught in 1964, and this permitted more extensive analysis of their flight activity.

***Phloeosinus* species.** A sharp increase in the population of these bark beetles was shown in the 1964 net samples, especially of the smaller species, *Phloeosinus punctatus*. Over 1,000 individuals of this species were collected during a single day in 1964. Seasonal dispersal activity was brief, however, since large numbers of this species were caught on May 15 and May 26, but only a few isolated beetles thereafter. *P. sequoiae* did not increase as greatly during the two seasons, but it was present in flight from May 26 to June 22, 1964.

Figure 20 depicts the typical diurnal flight patterns of these bark beetles. Both apparently reach their maximum daily flight densities during the mid-day or early afternoon hours. There was a definite indication that *P. punctatus* had a lower temperature threshold for flight activity than *P. sequoiae*. Several times its flight began at air temperatures of 64 to 66° F., whereas *P. sequoiae* was not caught when the air temperature was less than 68° F.

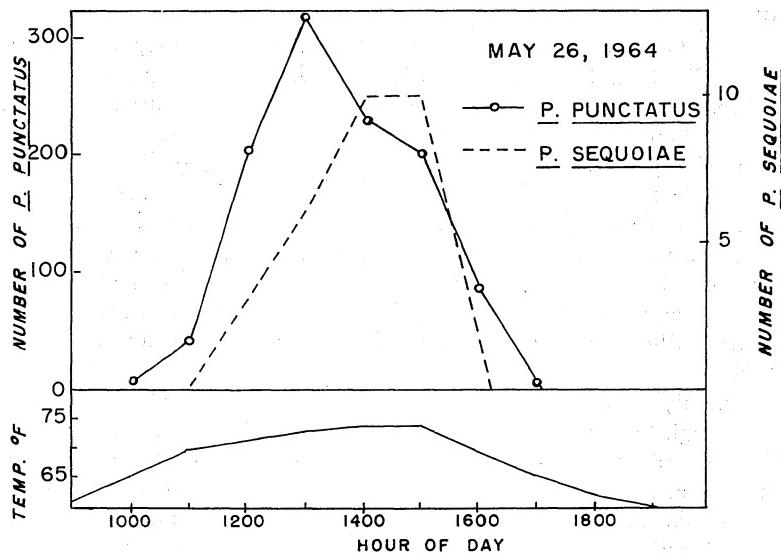


Figure 20. Daily flight patterns of *Phloeosinus* species.

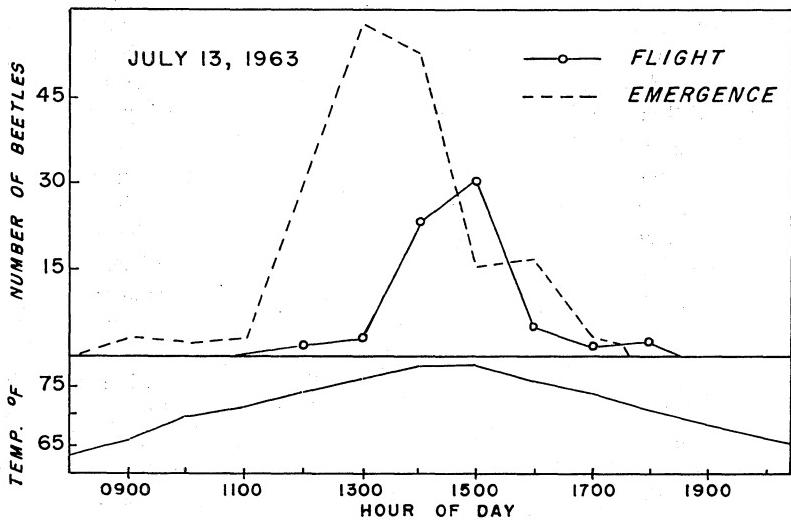


Figure 21. Daily emergence and flight activity of *Scolytus unispinosus*.

Table 12. MISCELLANEOUS SPECIES OF SCOLYTIDAE CAPTURED IN 1963 AND 1964

Species	Month caught	Temperatures at time of capture °F.
<i>Hylurgops rugipennis</i> (Mannerheim)	March-April	54-60
<i>Taenioglyptes pubescens</i> (Hopkins)	April-May	60-65
<i>Pseudohylesinus granulatus</i> (LeConte)	April-May	63-68
<i>Phloeosinus punctatus</i> LeConte	May	64-75
<i>Monarthrum scutellare</i> (LeConte)	May	66-73
<i>Alniphagus aspericollis</i> (LeConte)	May	73 ^{a1}
<i>Carphoborus vandykei</i> Bruck	May	65*
<i>Ips concinnus</i> (Mannerheim)	May	66*
<i>Leperisinus californicus</i> Swaine	May	72*
<i>Pseudohylesinus nobilis</i> Swaine	May-June	63-70
<i>Pseudohylesinus tsugae</i> Swaine	May-June	66-75
<i>Anisandrus pyri</i> (Peck)	May-June	65-76
<i>Xyleborus saxeseni</i> Ratzeburg	May-June	65-72
<i>Phloeosinus sequoiae</i> Hopkins	May-June	68-75
<i>Scolytus tsugae</i> (Swaine)	July-August	72-77

* Only one specimen caught or, if more, caught in the same collection.

Seasonal Differences

Certain significant seasonal differences were found. Many concerned the time of dispersal of the various species, which varies considerably because of different threshold temperatures. Initial occurrence and duration of flight depend upon favorable weather, which is normally sporadic and unpredictable for the area. Thus, knowledge of temperature thresholds provides some indication of when flights will occur, but accurate prediction is difficult because of the variable, highly fluctuating weather patterns of the region. The seasonal flight of *Pseudohylesinus nebulosus*, for example, was prolonged until the first week of May in 1963, whereas the peak flight of this species was completed by the end of March in 1962 and 1964. Large numbers of *Scolytus unispinosus* were not caught until mid-July in 1963, whereas peak flight activity was in progress by the third week of June in 1962 and 1964.

From the differences in seasonal flight rhythms of the various species for the three seasons, some generalizations can be made regarding the months of the year most favorable for flight. With the exception of *Pseudohylesinus nebulosus*, which may fly in considerable numbers in March, the most critical period for most of the species appears to be from late April through May and June. However, late May through July seems to be the most critical period for species requiring higher temperatures, such as *Hylastes ruber*, *Dryocoetes auto-*

graphus, and *Scolytus unispinosus*. Since *S. unispinosus* requires time in the spring to complete development to the adult stage, a temperature accumulation or "day degree" study might be of considerable aid in predicting seasonal flights of this species.

Other seasonal differences were undoubtedly linked with host availability and location during the two seasons. The great amount of windthrown timber available in 1963 provided the potential for an extensive population increase of scolytids. To judge by the numbers trapped in the rotary nets, this was particularly evident for *Pseudohylesinus nebulosus*, *Trypodendron lineatum*, *Dryocoetes autographus*, and *Phloeosinus* species. There was also a marked increase in the number of different species caught in 1964: A total of 15 species were identified from the 1963 net catches, whereas 25 species were caught in 1964. Most of the species not found in 1963 were probably present in too low numbers for detection by the sampling techniques used. The plentiful host supply in 1963 no doubt led to an increase in numbers sufficient to result in capture of a few specimens by the rotary nets.

There is also the possibility that the less abundant host supply in 1964 may have contributed to the greater number of species caught during that season. Forced to fly farther and longer to locate the less plentiful host material, the scolytids were perhaps more vulnerable to capture in the nets.

Displacement of host material by recent logging activities or storm damage was also believed to exert an influence on the time of dispersal flights. Certain species, such as *Pseudohylesinus nebulosus*, *P. grandis*, and *Trypodendron lineatum*, were caught in flight at somewhat lower temperatures in 1964 than in the previous year. A chief cause of this difference is believed to be the displacement of brood logs infested in 1963. As discussed previously, large groups of infested logs, felled by windstorm or logging operations, were exposed to direct solar radiation in the spring of 1964. Higher temperatures at these sites enabled the scolytids to initiate flight sooner than was possible from shaded sites. Once flight had begun in the warmer regions, it could continue into cooler areas, such as the experimental plot, where the beetles were caught in flight at lower air temperatures than thought necessary to initiate flight activity.

Variations in host availability and the displacement of brood logs infested the previous year can have profound influences on scolytid flight activity. Such factors should be considered when studying flight activity of bark beetles in relation to physical factors and when surveying a region for a particular species.

Summary and Conclusions

Temperature was found to be the primary factor governing flight activity. With the exception of *Scolytus unispinosus*, the initiation of seasonal flight depended on the occurrence of sufficiently high temperatures to induce flight of the various species. Since *S. unispinosus* overwintered in the larval stage, a period of time was required for completion of development before flight could occur the following season. A wide range of air temperatures necessary to initiate flight of the various species was observed. These differences in temperature thresholds (Table 13) resulted in a sequence in the temporal distribution of scolytid species in flight throughout the season.

Light intensity was also found to be influential in regulating the flight activity of bark beetles. For example, many of the day-flying species, such as *Pseudohylesinus nebulosus*, *P. grandis*, and *Trypodendron lineatum*, sharply decreased their flight activity in late afternoon and ceased activity at darkness even when temperatures remained optimal. Light intensities up to 8,500 foot-candles were recorded during flights of these species. In contrast, five species were found to have crepuscular patterns of daily flight. *Hylastes nigrinus*, *H. ruber*, *Gnathotrichus sulcatus*, *G. retusus*, and *Dryocoetes autographus* flew in greatest numbers between 1700 and 1900 hours. Light-intensity recordings indicated that intensities of 200-500 foot-candles were most favorable for flight activity of these species. Because of its exposed location, the illuminometer recorded maximum values of light intensity in the stand. Thus, the actual values of light intensity most favorable to the crepuscular species could be expected to be considerably lower than those cited.

Table 13. THRESHOLD AIR TEMPERATURES NECESSARY TO INITIATE FLIGHT ACTIVITY OF VARIOUS SCOLYTID SPECIES

Species	Flight threshold °F.
<i>Pseudohylesinus nebulosus</i>	54-55
<i>Pseudohylesinus grandis</i>	56-58
<i>Trypodendron lineatum</i>	58-60
<i>Hylastes nigrinus</i>	58-60
<i>Gnathotrichus sulcatus</i>	61-63
<i>Gnathotrichus retusus</i>	61-63
<i>Dryocoetes autographus</i>	65-68
<i>Hylastes ruber</i>	68-70
<i>Scolytus unispinosus</i>	68-72

Relative humidity within the range of values which occurred during the three seasons had no apparent effect on flight activity.

Winds were usually intermittent in the area. Recurrent breezes of velocities as low as 3 or 4 miles per hour curtailed flight activity of *Trypodendron lineatum*. However, activity of this species was not completely terminated with gusts as high as 3 to 10 miles per hour.

Olfactory response to an attractant was also found to be highly influential in governing flight activity. *T. lineatum*, a species known to produce a natural attractant, concentrated in high-flight densities in local areas containing attractive material. This behavior noticeably affected net catches, which varied according to the proximity of the attractive material. It is recommended that this factor be further investigated for other species as well as *T. lineatum*. There was also an indication that host logs *per se* might be attractive to some of the species.

Certain noteworthy seasonal differences in scolytid flight were observed during the 1963 and 1964 seasons. In 1964, certain species were captured in flight at temperatures somewhat lower than had been found necessary the previous year. It is probable that flight was recorded at lower air temperatures at the research area in 1964 because of the extensive number of brood logs exposed on unshaded sites. The temperatures listed in Table 13 are representative of the values necessary to induce flight of the respective species from shaded sites in the forest. The effect of the predominantly higher temperatures at exposed, unshaded sites was exemplified by comparing emergence of beetles from shaded logs and from logs placed in clearcut areas of the forest. Emergence from the clearcut areas preceded that of the shaded sites by as much as five weeks.

Larger numbers of certain bark beetles as well as a greater variety of species were caught in the traps in 1964 than in 1963. It is thought that these increases in quantity and variety were primarily due to the great abundance of fresh host material available to the 1963 flights. Conversely, the limited host supply in 1964 may have rendered beetles more vulnerable to capture, since dispersal flights were conceivably more sustained in order to locate the less plentiful host material.

There is a strong indication that the type of diurnal flight pattern exhibited by a particular species is characteristic of that genus. For example, two species of *Phloeosinus* and both *Pseudohylesinus* species were day flyers, whereas two *Gnathotrichus* and two *Hylastes* species were evening flyers. This aspect would require a more extensive survey of a greater number of species to be conclusive.

Temporal distribution of species in seasonal flight permits some statements regarding interspecific competition among the bark beetles.

The earlier flights of *Pseudohylesinus nebulosus* allow that species to preempt the more destructive Douglas-fir beetle in those portions of the host suitable to both. *P. grandis*, found in flight slightly later than *P. nebulosus*, falls in the same category. In contrast, flights of *Dryocoetes autographus* occur too late in the season for that species to effectively compete with the major colonization of the Douglas-fir beetle for available host material. The late dispersal flights of *Scolytus unispinosus* also place that species in the latter category.

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